LIFE HISTORY OF THE RARE RED ALGA *TSENGIA BAIRDII* (= *PLATOMA BAIRDII*) (NEMASTOMATACEAE, RHODOPHYTA) FROM SCOTLAND

Christine A. MAGGS

School of Biology and Biochemistry, The Queen's University of Belfast, Medical Biology Centre Belfast BT9 7BL, Northern Ireland (e-mail: c.maggs@qub.ac.uk)

ABSTRACT — A single thallus of the rare red seaweed *Tsengia bairdii* (Farlow) K. Fan *et* Y. Fan (= *Platoma bairdii* (Farlow) Kuckuck) (Nemastomataceae) was collected on a subtidal pebble on the west coast of Scotland. The terete gelatinous axes, which were only 7 mm high, were monoecious. They bore numerous cystocarps and a few spermatangia, which represent the first observation of male structures in this genus. Released carpospores grew into expanded basal discs that gave rise to erect axes bearing irregularly cruciate tetrasporangia. Irregularly cruciate to zonate tetrasporangia were also formed on these basal discs. Karyological studies on dividing tetrasporocytes showed about 25 bodies, identified as paired meiotic chromosomes on the basis of their size in comparison to mitotic and meiotic chromosomes in other red algal species. These observations confirm the isomorphic life history inferred from early field collections and show that this species is monoecious. *Tsengia bairdii* is an extremely rare seaweed in Europe -- it seems to be confined to sublittoral cobbles and has a temporally patchy distribution.

RÉSUMÉ — Un unique thalle de l'algue, rare, *Tsengia bairdii* (Farlow) K. Fan *et* Y. Fan (= *Platoma bairdii* (Farlow) Kuckuck) (Nemastomataceae), a été récolté sur un galet infralittoral, sur la côte ouest de l'Ecosse. Les axes gélatineux de section arrondie, de 7 mm de haut seulement, étaient monoïques. Ils portaient de nombreux cystocarpes et quelques spermatocystes ; ces derniers constituent la première observation de structures mâles chez ce genre. Les carpospores sont développés en des disques basaux étendus qui ont produit des axes dressés portant des tétrasporocystes irrégulièrement cruciés. Des tétrasporocystes, irrégulièrement cruciés à zonés, ont aussi été produits par les disques basaux. Des études caryologiques sur les tétrasporophytes en division ont mis en évidence environ 25 corpuscules, identifiés, sur la base de leur taille, comparativement aux chromosomes méïotiques ou mitotiques des autres algues rouges, comme des chromosomes méïotiques appariés. Ces observations confirment le cycle de vie isomorphe déduit de premières récoltes dans la nature et montrent que cette espèce est monoïque. *Tsengia bairdii* est une algue extrêmement rare en Europe - il semble confiné aux galets infralittoraux et sa distribution est morcellée dans le temps. (Traduit par la Rédaction)

KEY WORDS: Life history, Nemastomataceae, pebbles, *Platoma*, rare algae, Rhodophyta, *Tsengia bairdii*

INTRODUCTION

As part of the Marine Nature Conservation Review of Great Britain, currently being undertaken by the Joint Nature Conservation Committee, the marine communities of 86 Scottish sealochs were surveyed over a four-year period (Howson *et al.*, 1994). In July and August 1988 the sealochs of the Hebridean island of Lewis and Harris were examined in order to describe the marine habitats and communities present and to asssess their nature-conservation importance (Howson, 1988). At the mouth of a sealoch on the west coast of Lewis, an interesting community of ephemeral algae was observed on sublittoral pebbles. One of these species was *Tsengia bairdii* (Farlow) K. Fan *et* Y. Fan, a member of the Nemastomataceae more generally known as *Platoma bairdii* (Farlow) Kuckuck (see Masuda & Guiry, 1995). This rare species has never been observed *in situ* in the British Isles; the only previous British record was of a drift thallus collected in 1857 in Northumberland, on the north-eastern coast of England (Batters, 1900; Dixon & Irvine, 1977). Although its morphology and female reproductive development have been described in great detail, based on material from Helgoland, North Sea (Kuckuck, 1912), *T. bairdii* has never previously been grown in culture. The present paper therefore concentrates on the ecology of this species and its life history in culture.

MATERIALS AND METHODS

The site where *Tsengia bairdii* was collected (Fig. 1) is on the eastern side of the islet of Greine Sgeir (United Kingdom National Grid Reference NB 012 155) outside the mouth of Loch Resort but sheltered from the west by the island of Scarp. There is no road access to much of the west coasts of Lewis and Harris, so the survey was carried out using a schooner with inflatable boats as diving platforms. Subtidal algal communities were studied at this site on 3 August 1988 by SCUBA diving; samples were examined live with dissecting microscopes on board the schooner.

Field-collected algal material was fixed in 4 % seawater-Formalin, stained with 1 % aniline blue, post-fixed in dilute HCl and mounted in Karo® corn syrup. Cultured material was studied live or fixed in 1:1 acetic acid:ethanol and stained in Wittman's haematoxylin as described by Maggs & Rico (1991). Chromosomes were examined by squashing dividing tetrasporocytes in haematoxylin and counted by photographing and drawing them in different planes of focus.

One cystocarpic axis of *Tsengia bairdii* was transported back to the laboratory alive in seawater. It was placed in modified von Stosch's medium (Guiry & Cunningham, 1984) on a glass half-slide in a small petri dish for three weeks under low light conditions (ca. 10 µmol photons $m^{-2} s^{-1}$) at 12° C, 16:8 h light:dark, until small discs were observed on the glass. Some contaminating algae were wiped off repeatedly until the culture appeared to be unialgal.

Slide mounts of field-collected and cultured material have been deposited in the herbarium of The Natural History Museum, London.

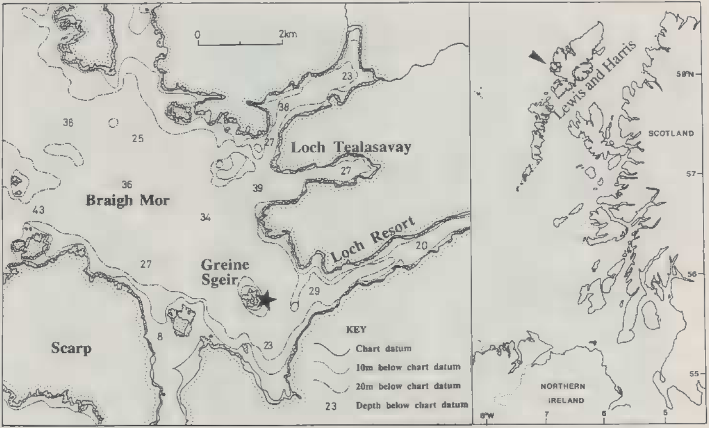


Fig. 1. Chart showing collection site (star) for *Tsengia bairdii* with a map of western Scotland (right) indicating the location of the enlarged area (arrow).

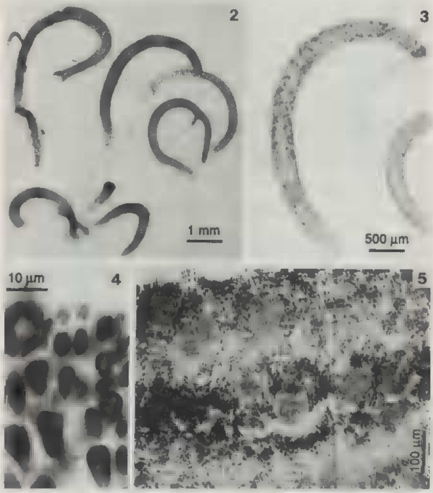
OBSERVATIONS

The Greine Sgeir site (Fig. 1) consisted underwater of a rocky reef with some vertical faces descending rapidly to a gently sloping bed of *Phymatolithon calcareum* (Pallas) W. Adey *et* McKibbin maërl at 9-12 m depth, where there was a wide variety of epiphytic algae such as *Dudresnaya verticillata* (Withering) Le Jolis, *Dictyota dichotoma* (Hudson) Lamouroux, *Compsothamnion thuyoides* (J. Smith) F. Schmitz and *Bonnemaisonia asparagoides* (Woodward) C. Agardh. *Schmitzia neapolitana* (Berthold) Lagerheim *ex* P.C. Silva occurred on stones and one thallus of *Dermocorynus montagnei* P. Crouan *et* H. Crouan with cystocarps was collected on a pebble. The maërl bed sloped down to a clean cobble and sand bottom at about 15 m below Chart Datum. Scattered individuals of *Laminaria hyperborea* (Gunnerus) Foslie occurred on more stable substrata such as boulders. A fairly high diversity of algae was observed on the cobbles, including common species such as *Haraldiophyllum bonnemaisonii* (Kylin) A. Zinova, *Lomentaria clavellosa* (Turner) Gaillon and *Cryptopleura ramosa* (Hudson) Kylin *ex* Lily Newton. A single individual of *Tsengia bairdii* was collected on an otherwise bare small pebble.

The *Tsengia bairdii* thallus was composed of an expanded disc ca. 5 mm in diameter with a group of 10 erect axes that were 4-7 mm in length and strongly recurved towards the substratum (Fig. 2). The axes were gelatinous, bright pink, terete and 200-270 μm in diameter. Mostly of the axes were simple but two of them had a short lateral branch, one being near the apex and resulting in a slightly compressed axis. Numerous small cystocarps were present along the entire length of the axes (Figs 3, 4), visible through the filamentous cortex (Fig. 3).

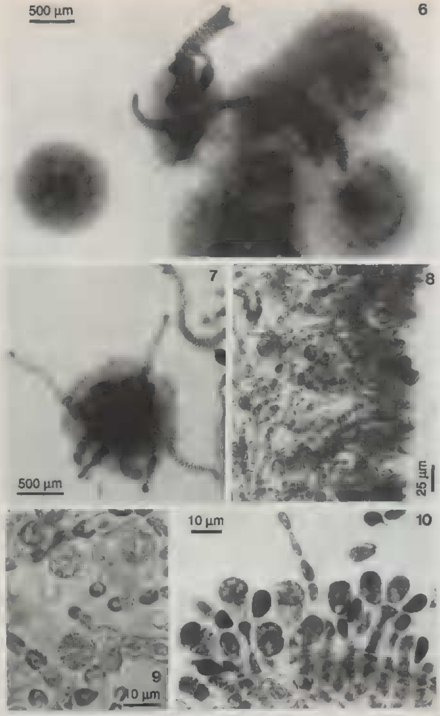
Terminal cells of the cortical filaments bore a few hairs, and cells from which hairs had been shed previously were enlarged and deeply staining. These latter cells superficially resembled gland cells, but some stained remnants of hair walls could be seen attached to their apices. The thallus was monoecious. Spermatangia (Fig. 4) occurred very sparsely among cortical cells, borne singly on ovoid spermatangial mother cells measuring c. 6.5 x 3 μm. They developed from a protuberance formed at the distal end of the mother cell; the protuberance appeared to cleave transversely but spermatangia were so rare that this interpretation requires confirmation. Spermatangia (Fig. 4) varied in shape from almost spherical to ovoid, 3 μm in diameter and up to 6 μm in length. Released spermatia, of which very few were observed, were spherical and 3 μm in diameter. Neither fertilized nor unfertilized carpogonial branches or auxiliary cells were observed and tetrasporangia were not present on erect axes.

Cultured discs, presumably initiated from released carpospores, were grown for two months at 12° C, 16:8 h, in dim red light (to reduce the growth of possible brown algal contaminants) until they were up to 250 μm in diameter. Early stages of development could not be studied due to the very small numbers of sporelings present. The discs were roughly circular with non-pigmented margins, as is typical of crustose red algae and basal discs, and some loose filamentous growths. Following transfer to white light, the discs grew more rapidly, with distinct radial filaments, and were 0.9-2.0 mm in diameter 2 months later. They then formed small erect axis initials centrally. Two weeks after the erect axes were first noted, up to 14 axes had developed in a dense central cluster on each disc (Fig. 6). The erect axes were up to 1.2 mm in length, strongly recurved, simple or with forked branching. They were mostly terete with one slightly flattened axis, and they were of looser construction than the field-collected material (Fig. 7).

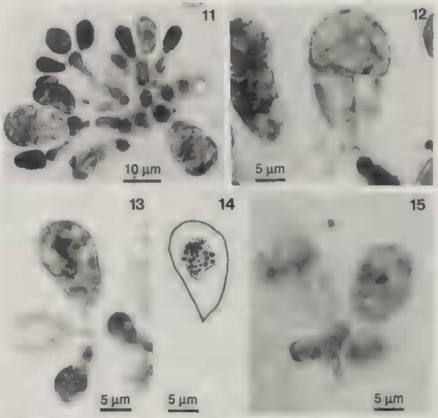


Figs 2-5. Field-collected material of *Tsengia bairdii*. Fig. 2. Several recurved erect axes removed from holdfast, showing very sparse branching. Fig. 3. Erect axis with numerous cystocarps visible among cortical filaments. Fig. 4. Squash of cortical filaments showing two spermatangia, each borne singly on spermatangial mother cell. Fig. 5. Squash of cystocarpic axis with numerous small cystocarps among dense cortical fascicles.

When the erect axes were 5 weeks old, they started to produce numerous sporangia (Fig. 8). These sporangia were terminal on cortical filaments (Fig. 9), were more or less spherical, (6-)11-12 µm in diameter, and were divided once in an oblique plane, resembling bisporangia, or had divided again to form irregularly cruciate tetrasporangia (Fig. 9).



Figs 6-10. *Tsengia bairdii* in culture. Fig. 6. Compact basal discs with obvious radial patterns bearing central clusters of erect axes, 2 weeks after initiation of erect axes. The isolated disc on the left has just developed erect axis initials. Fig. 7. The same basal disc shown on left in Fig. 6 after 2 weeks further growth, bearing a group of loose filamentous erect axes. Fig. 8. Squash of cortex of erect axis showing numerous spherical tetrasporangia. Fig. 9. Detail of terminal tetrasporangia from erect axis. Fig. 10. Squash of part of basal disc showing compact lower layers and superficial filaments bearing developing tetrasporangia.



Figs 11-15. Development of tetrasporangia on basal disc of *Tsengia bairdii* in culture. Fig. 11. Terminal tetrasporangia at various stages of development, some borne trichotomously. Fig. 12. Mature cruciately divided tetrasporangium. Fig. 13. Tetrasporocyte with a central homogeneous nuclear zone containing densely staining bodies interpreted as paired meiotic chromosomes. Fig. 14. Drawing of same tetrasporocyte, indicating chromosomes shown in Fig. 13 (solid dots) and those seen in other planes of focus (open circles) which total 25. Fig. 15. Tetrasporocyte at metaphase, showing oblique plane of metaphase plate and initiation of first oblique cell division.

Tetrasporangia were formed on the basal discs also (Figs 10-12). The basal discs were quite firm in texture, but lacked any secondary pit connections or cell fusions, and the tetrasporangia were usually formed on filaments that protruded above the surface of the disc (Fig. 10). These filaments terminated in dichotomies or trichotomies (Figs 10, 11), each branch of which could develop into ■ sporangium or a sterile filament. Sterile paraphysis-like filaments were also formed from the basal disc among the fertile filaments (Fig. 10). Tetrasporangia were mostly ovoid, 15.5-25 µm long x 10.5-13 µm wide, varying from cruciately to irregularly zonately divided (Figs 10-12). They were thus considerably larger than those formed on the erect axes.

Karyological studies on dividing tetrasporocytes showed distinct chromosome-like bodies within the homogeneous nuclear area (Figs 13, 14) which later aggregated into an obliquely orientated metaphase plate (Fig. 15). During division, there were about 25 haematoxylin-stained bodies that were identified as paired meiotic chromosomes on the basis of their size in comparison to mitotic and meiotic chromosomes in other red algal species.

Release of spores was not observed and further observations were not possible because the culture became overgrown by contaminants, which probably arose from spores of macroalgal endophytes present in the original collection.

DISCUSSION

The morphology of the Scottish plant corresponds closely to the Helgoland material of *Tsengia bairdii* illustrated by Kuckuck (1912, as *Platoma*). It is significant that Kuckuck (1912) collected both small terete thalli (pl. 10, fig. 1), similar in size to the Scottish material, and large, flattened blades up to 16 cm long (pl. 9) resembling the type collection from Martha's Vineyard, Massachusetts, U.S.A. (Kuckuck, 1912, figs 4-6). Thus, although the Scottish material differs greatly in size and habit from the type specimen, there is no reason to doubt its identification as *T. bairdii*. The wide variation in size found in this species may be related to environmental conditions. Sears & Wilce (1975) reported that at Cape Cod, Massachusetts, conspicuous erect axes appeared to be restricted to deep water and only basal discs were observed in shallow water. Kuckuck (1912), by contrast, found the largest plants in the lower intertidal of Helgoland.

The habitat of *T. bairdii* in the British Isles, on sublittoral stones with moderate wave exposure, appears to be similar to that reported elsewhere in Europe and North America. Kuckuck's find of lower-shore populations at the island of Düne near Helgoland represents the only record of this species in the intertidal zone. This habitat unfortunately no longer exists due to building work at the beginning of the Second World War (Kornmann & Sahling, 1977; K. Lüning, personal communication). Very few observations of attached rather than drift plants have ever been made, and all other collections were on sublittoral stones. Kornmann & Sahling (1977) did not give any specific depths for the the two collections made *in situ* at Helgoland, while Lüning's (1970) Helgoland specimen was found at 7 m. In Denmark, Rosenvinge (1917) dredged small plants on granitic pebbles from a stony bottom at 20 m and at Cape Cod *T. bairdii* grew on stones at 1-22 m (Sears & Wilce, 1975).

The observation of *T. bairdii* in Scotland in August is typical of the phenological pattern for this species in Europe, where it seems to be a summer annual, having been collected only in May to September. Basal discs without erect axes have never been observed in Europe. The phenology of *T. bairdii* is known best from Cape Cod (Sears & Wilce, 1975), where this species was observed from January to August, overwintering as crustose "juveniles" that gave rise to erect axes in early spring. Tetrasporangia were recorded in January, April-May and July-August. Cystocarps occurred in July and August only, when the water temperature was at its maximum of 16-22° C.

The geographical distribution of *T. bairdii*, from Nova Scotia (Edelstein *et al.*, 1967) to Massachussetts in the western North Atlantic and from Denmark to Scotland in the eastern North Atlantic, indicates that it has a wide temperature tolerance. At Cape Cod, winter temperatures are below 0° C, whereas summer temperatures reach 22° C. Helgoland in the North Sea also experiences large temperature ranges, with mean monthly temperatures of 3° C in February and 18° C in August (Anonymous, 1962). By contrast, the Scottish site has a relatively narrow annual temperature range, from 7.5 to 13.5° C (Lee & Ramster, 1981). The attribution to this species of non-reproductive material from Tenerife (Afonso-Carrillo *et al.*, 1984) requires re-investigation as the occurrence of *T. bairdii* in the Canary Islands would represent a considerable southward range extension from the British Isles.

The extreme scarcity of records of *T. bairdii* is very unlikely to be due to its having been overlooked because the present author has microscopically surveyed sublittoral pebbles from numerous sites in Ireland, Scotland and Wales for over 15 years. Even in the absence of any erect axes, the basal discs are distinct from other red algae with isomorphic or heteromorphic life histories that involve crustose stages (see lists in Maggs, 1990). Of those crusts that resemble *T. bairdii* in lacking cell fusions and secondary pit connections, only a few also have parallel radiating basal layer filaments like *T. bairdii*. These species, *Cruoria cruoriaeformis* (P. Crouan *et* H. Crouan) Denizot, *Cruoria pellita* (Lyngbye) Fries and *Haemescharia hennedyi* (Harvey) Vinogradova, all have erect filaments embedded in a mucilaginous matrix and additional prostrate filaments interwoven between them. By contrast, *T. bairdii* basal discs have a firm texture and lack prostrate filaments other than the basal layer itself.

The total of only two thalli of *T. bairdii* ever collected in the British Isles means that it is probably the rarest macroalgal species known in this geographical area. Its extreme rarity in the British Isles clearly merits "nationally rare" Red Data Book status, which for benthic marine organisms is defined by presence in eight or fewer 10 km grid squares (Sanderson, 1996). Elsewhere in Europe, it is not much more common. In Denmark, during his assiduous study of pebble communities by dredging, Rosenvinge (1917) made only a single collection of this species; likewise, in Helgoland, Kornmann & Sahling (1977) found *T. bairdii* only four times over a 17-year period during which the local algae were studied intensively.

Tsengia bairdii is generally very rare in North America also: Farlow (1875) described the species from a single specimen and in Nova Scotia only one thallus has ever been found (Edelstein *et al.*, 1967). However, this species can sporadically be much more frequent in New England. Taylor (1941) discovered many drift specimens at Martha's Vineyard in 1940, whereas he had failed to observe it there during the previous 20 years. In a very detailed populational study of *T. bairdii*, at Cape Cod, Sears & Wilce (1975) found a temporally patchy distribution: it seemed to be absent in some years from areas in which it had occurred in previous years. When present, however, it was relatively common. Basal discs were present on 4 % and 10 % of sublittoral stones collected at, respectively, 1-22 m depth from the SW tip of Martha's Vineyard and a pair of sites on the north coast of Martha's Vineyard and the adjacent Cape Cod coast. These observations suggest that the reappearance of *T. bairdii* in its type locality after an absence of 70 years (Taylor, 1941) can best be explained by its persistence as inconspicuous basal discs.

Platoma bairdii was transferred to the genus *Tsengia* by Fan & Fan (1962) because it differed from the type species of *Platoma*, *P. cyclocolpa* (Montagne) F. Schmitz, and the other species then included in the genus (see Masuda & Guiry, 1995), in its female reproductive development, the lack of gland cells, and because it formed tetrasporangia on upright thalli. In Scottish *T. bairdii*, the stained basal remnants of hair cells sufficiently resembled gland cells to cause confusion, but were typical of red algal hair cells which always contain dense cytoplasm (Cabioch, 1972, p. 164, 166). The type specimen of *T. bairdii* has tetrasporangia (Farlow, 1975; Kuckuck, 1912), and Taylor (1941) noted only tetrasporangial plants in his collection. Kuckuck (1912) found tetrasporophytes and females bearing cystocarps, and also some thalli with tetrasporangia, carpogonia and cystocarps. In contrast, Rosenvinge (1917) reported that tetrasporangia and cystocarps were borne on distinct invidividuals and mixed-phase reproduction was not observed.

Spermatangia were previously unknown in this genus. The observation of spermatangia in the cystocarpic Scottish material indicated that *T. bairdii* is monoecious. Spermatangia were extremely inconspicuous, however, and could easily have been overlooked in previous morphological studies. The present life-history study has confirmed that carpospores formed by cystocarps borne on erect axes give rise to thalli that form tetrasporangia on erect axes. Karyological observations suggest that tetrasporangia are meiotic and that the haploid chromosome number is about 25. Although no comparative data are available for the Nemastomataceae, karyological studies of the Gigartinales have usually shown haploid chromosome complements of 24-34 (Cole, 1990) so this chromosome number would be quite typical of the order. The formation in *T. bairdii* of tetrasporangia on the basal discs as well as in erect axes is probably unique among the non-coralline red algae. In the Corallinales, it occurs in some species that form basal crusts, which give rise to erect branches that break off and form maërl (Cabioch, 1970). As the Corallinales is probably one of the oldest florideophyte orders (Freshwater *et al.*, 1994; Ragan *et al.*, 1994), this life-history feature may be a primitive trait but the lack of life-history studies in the genus *Tsengia* means that it would be unwise to draw elaborate conclusions without further data. Nevertheless, the life history of *T. bairdii*, with elements of both an isomorphic and a heteromorphic pattern, provides further evidence of the complexity of life histories in the red algae (West & Hommersand, 1981).

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REFERENCES

AFONSO-CARRILLO M.C., GIL-RODRIGUEZ M.C., HAROUM TABRAUE R., VILLENA BALSA M. & WILDPRET DE LA TORRE W., 1984 — Adiciones y correcciones al catalogo de algas marinas bentonicas para el archipielago canario. *Vieraea* 13: 27-49.

ANONYMOUS, 1962 — *Mean monthly temperature and salinity of the surface layer of the North Sea and adjacent waters, 1905-54*. Copenhagen, ICES.

BATTERS E.A.L., 1900 — New or critical British marine algae. *Journal of Botany, London* 38: 369-379.

CABIOCH J., 1972 — Etude sur les Corallinacées. II. La morphogenèse, conséquences systématiques et phylogénétiques. *Cahiers de Biologie Marine* 13: 137-287.

CABIOCH J., 1970 — Le maërl des côtes de Bretagne et le problème de sa survie. *Pen ar Bed* 7: 421-429.

COLE K.M., 1990 — Chromosomes. *In*: Cole K.M. & Sheath R.G. (eds) *Biology of the red algae*. Cambridge, Cambridge University Press, pp. 73-102.

DIXON P.S. & IRVINE L.M., 1977 — *Seaweeds of the British isles Volume 1 Rhodophyta Part 1 Introduction, Nemaliales, Gigartinales*. London, British Museum (Natural History), 252 p.

EDELSTEIN T., McLACHLAN J. & CRAIGIE J.S., 1967 — Investigations of the marine algae of Nova Scotia. II. Species of Rhodophyceae new or rare to Nova Scotia. *Canadian Journal of Botany* 45: 193-202.

FRESHWATER D.W., FREDERICQ S., BUTLER B.S., HOMMERSAND M.H. & CHASE M.W., 1994 – A gene phylogeny of the red algae (Rhodophyta) based on plastid *rbcL*. *Proceedings of the National Academy of Sciences, USA* 91: 7281-7285.

GUIRY M.D & CUNNINGHAM E.M., 1984 — Photoperiodic and temperature responses in the reproduction of north-eastern atlantic *Gigartina acicularis* (Rhodophyta: Gigartinales). *Phycologia* 23: 357-367.

HOWSON C.M., 1989 — *Surveys of Scottish sealochs. Sealochs of the Isles of Harris and Lewis. Nature Conservancy Council, Chief Scientists' Directorate Report No. 982*. Peterborough, NCC.

HOWSON C.M., CONNOR D.W. & HOLT R.H.F., 1994 — *The Scottish sealochs. An account of surveys undertaken for the Marine Nature Conservation Review. Joint Nature Conservation Committee Report No. 164*. Peterborough, JNCC.

KORNMANN P. & SAHLING P.-H., 1977 — Meeresalgen von Helgoland. Benthische Grün . Braun — und Rotalgen. *Helgoländer wissenshaftliche Meeresuntersuchungen* 29: 1-289.

KORNMANN P. & SAHLING P.-H., 1994 – Meeresalgen von Helgoland. Zweite Ergänzung. *Helgoländer Meeresuntersuchungen* 29: 1-289.

KUCKUCK P., 1912 - Beiträge zur Kenntnis der Meeresalgen. 12. Über *Platoma bairdii* (Farl.) Kck. *Wissenshaftliche Meeresuntersuchungen, Neue Folge, Abteilung Helgoland* 5: 187-208.

LEE A.J. & RAMSTER J.W., 1981 - *Atlas of the Seas around the British Isles*. Lowestoft, Ministry of Agriculture, Fisheries and Food.

LÜNING K., 1970 Tauchuntersuchungen zur Vertikalverteilung der sublitoralen Helgoländer Algenvegetation. *Helgoländer wissenshaftliche Meeresuntersuchungen* 21: 271-291.

MAGGS C.A., 1990 — Distribution and evolution of non-coralline crustose red algae in the North Atlantic. *In*: Garbary, D.J. & South, G.R. (eds) *Evolutionary biogeography of the marine algae of the North Atlantic*. Berlin, Springer-Verlag, pp. 241-264.

MAGGS C.A. & RICO J.M., 1991 – Karyological evidence of meiosis in *Gelidium latifolium* (Gelidiaceae, Rhodophyta) from Ireland. *Phycologia* 30: 487-494.

MASUDA M. & GUIRY M.D., 1995 — Reproductive morphology of *Itonoa marginifera* (J. Agardh) gen. et comb. nov. (Nemastomataceae, Rhodophyta). *European Journal of Phycology* 30: 57-67.

RAGAN M.A., BIRD C.J., RICE E.L., GUTTELL B.R., MURPHY C.A. & SINGH R.K., 1994 — A molecular phylogeny of the marine red algae (Rhodophyta) based on the nuclear small-subunit rRNA gene. *Proceedings of the National Academy of Sciences, USA* 91: 7276-7280.

ROSENVINGE L.K., 1917 — The marine algae of Denmark. Contributions to their natural history. Part II. Rhodophyceae II. (Cryptonemiales). *Kongelige Danske Videnskabernes Selskabs Skrifter, 7 Raekke, Naturvidenskabelig of Mathematisk Afdeling* 7: 153-284.

SANDERSON W.G., 1996 — *Rare marine benthic flora and fauna in Great Britain: the development of criteria for assessment. Joint Nature Conservation Committee Report no 240*. Peterborough, JNCC.

SEARS J.R. & WILCE R.T., 1975 – Sublittoral, benthic marine algae of southern Cape Cod and adjacent islands: seasonal periodicity, associations, diversity, and floristic composition. *Ecological Monographs* 45: 337-365.

TAYLOR W.R., 1941 — Reappearance of rare New England marine algae. *Rhodora* 43: 72-74.

TAYLOR W.R., 1957 — *Marine algae of the northeastern coast of North America*, ed. 2. Ann Arbor, University of Michigan Press, 509 p.

WEST J.A. & HOMMERSAND M.H., 1981 -- Rhodophyta: life histories. *In*: Lobban, C.S. & Wynne, M.J. (eds) *The Biology of Seaweeds*. Oxford, Blackwell Scientific, pp. 133-193.